"Stick 'n' peel": explaining unusual patterns of disarticulation and loss of completeness in fossil vertebrates.

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Few fossil vertebrate skeletons are complete and fully articulated. Various taphonomic processes reduce the skeletal fidelity of decaying carcasses, the effects of most of which are reasonably well understood. Some fossil vertebrates, however, exhibit patterns of disarticulation and loss of completeness that are difficult to explain. Such skeletons are one of two variants. They are incomplete, often markedly so, but the preserved parts are highly articulated. Alternatively, they are complete, or nearly so, but articulation varies markedly between parts of the body. A characteristic feature is the absence of skeletal elements that, on the basis of their larger size and/or greater density, would be predicted to be present. Here we erect a model, termed "stick 'n' peel", that explains how these distinctive patterns originate. The model emphasizes the role of decay products, especially fluids released from the carcass while resting on the sediment surface. These fluids permeate the sediment below and around the carcass. As a result, skeletal elements on the downward facing side of the carcass become adhered to the sediment surface, and are less likely to be remobilized as a result of current activity than others. The pattern of articulation and, especially, completeness is thus not what would be predicted on the basis of the size, shape and density of the skeletal elements. The effects of stick 'n' peel are difficult to predict *a priori*. Stick

'n' peel has been identified in vertebrate fossils in lacustrine and marine settings and is likely to be a common feature of the taphonomic history of many vertebrate assemblages. Specimens becoming adhered to the substrate may also explain the preservation *in situ* of the multi-element skeletons of invertebrates such as echinoderms, and integumentary structures such as hair and feathers in exceptionally preserved fossils.

KEYWORDS vertebrate taphonomy, disarticulation, completeness, biostratinomic processes, current transport, skeleton

1. Introduction

As a vertebrate carcass decays loss of skeletal fidelity is almost inevitable. As a result, most fossil vertebrate skeletons exhibit some combination of disarticulation and loss of completeness, as bones separate from, and are then removed from, the remainder of the carcass. The extent of any disarticulation and loss of completeness can be described qualitatively (Soares 2003) or using semi-quantitative (Beardmore et al. 2012a, b) or more fully quantitative methods (McNamara et al. 2011).

Disarticulation of individual bones or a series of co-joined bones (a unit such as a limb) is a pre-requisite for, but does not always result in, loss of completeness. Other that this basic tenet, it can be difficult to identify the specific processes that were responsible for loss of skeletal fidelity in a vertebrate fossil. Some processes, for example scavenging of carcasses, may leave distinctive taphonomic signatures (see Madgwick and Mulville 2015, and references therein), but many do not. The taphonomic history of a carcass after death and before final burial can be extremely complex. Carcasses may be subjected to multiple taphonomic processes acting in tandem or in sequence. Even subtle variations in external environmental parameters can impact on whether, and how, disarticulation and loss of completeness occurs. For example, variables such as water temperature and hydrostatic pressure impact on whether a carcass floats before settling to the sediment-water interface, and/or refloats after the build up of decay gases internally (see review by Reisdorf et al. 2012).

Hydrodynamic sorting of bones due to water current activity is a common cause of the disarticulation and loss of completeness the skeletons of vertebrate carcasses can experience before burial. This process occurs in both continental and marine environments. Continental environments include terrestrial land surfaces, fluvial systems and lakes that may be permanent or temporary. The carcass may be transported by the current, or currents pass over a carcass that remains *in situ.* Tidal, fluvial, floodplain and marginal lacustrine settings may experience regular or episodic changes

63 in water level that leave carcasses alternately resting on the sediment-water, and sediment-air,
64 interface on various timescales.

65 In the past few decades, substantial progress has been made in understanding how current
66 activity reduces the completeness and articulation of skeletons. It has long been recognised (Boaz
67 and Behrensmeyer 1976) that field (Nasti 2005) and laboratory based experiments are invaluable in
68 resolving how the skeletal fidelity of a carcass can be reduced by current activity (see Peterson and
69 Bigalke 2013). The scenario that has been investigated most frequently is how isolated bones are
70 transported by water currents. Experimental studies repeatedly confirm that the processes involved
71 are not just complex, but even unpredictable. Size, shape, mass and density are key variables that
72 can be quantified for individual bones. The interaction of such variables makes it difficult to predict
73 *a priori* exactly how individual bones will behave in a current (Voorhies 1969; Boaz and
74 Behrensmeyer 1976; Blob 1997, Trapani 1998, Peterson and Bigalke 2013).

75 Skeletons need not be reduced first to individual bones then transported. Transport of a
76 freshly killed carcass tends not to result in its disarticulation and loss of completeness, i.e., during
77 the first of the three unit-phases of fluvial transport defined by Nawrocki et al. (1997). As noted by
78 Haglund and Sorg (2002) relatively few experimental studies have attempted to simulate scenarios
79 between the end member conditions of 'freshly killed' and 'reduced to isolated skeletal elements':
80 i.e. how current activity impacts carcasses at different stages during progressive decay of their non-
81 biomineralised tissues (the non-skeletonised tissues). Attempts include the simulation of the
82 transport of defleshed but articulated limbs (reconstructed by wiring together bones that would
83 have been juxtaposed in life (e.g. Coard and Dennell 1995)). Forensic studies including experiments
84 with analogues, and the study of human remains recovered from aquatic settings, have provided
85 information on the various variables, including transport, that act in concert to reduce skeletal
86 fidelity (Anderson and Bell 2014, and references therein). The taphonomy of carcasses in fluvial
87 systems has been reviewed by Evans (2013).

88 In this study, we identify and demonstrate the significance of another variable: how
89 disarticulation and loss of completeness of the skeleton is influenced by whether the carcass
90 becomes adhered to the substrate in advance of being exposed to current activity. Aspects of this
91 phenomenon, which we term "stick 'n' peel", have been noted by previous authors, for example
92 Bickart (1984), Trewin and Davidson (1996) and Mayr (2001). A generalised model that considers the
93 mechanisms by which stick 'n' peel forms has, however, not been developed. We present this first,
94 then use a series of existing and new examples to define a series of criteria by which the presence of
95 stick 'n' peel can be tested for in fossil material. These examples demonstrate that stick 'n' peel

96 occurs in a wide range of fossil taxa preserved in various different environmental settings. This
97 indicates that it is likely to be a recurrent feature of the taphonomic history of vertebrate fossils, and
98 merits further study. Problematically, some of the features produced in vertebrate skeletons as a
99 result of stick 'n' peel can also be produced by other taphonomic processes.

100 **2. Mechanisms for the genesis of stick 'n' peel textures**

101 It has long been recognised that carcasses can become adhered to microbial mats coating
102 the sediment-water interface (see Hellawell and Orr 2012, and references therein). A classic
103 example of how this can influence disarticulation and loss of completeness is the fish illustrated by
104 Viohl (1990, fig. 2; see also Mayr 1967 and Seilacher et al. 1985). The vertebral column of the fish
105 recurved dorsally while it lay on the sediment surface in response to the osmotic effects of the
106 hypersaline water. Before it did so, the carcass had adhered to the microbial mat. The tail thus
107 remained *in situ* and fully articulated, when the vertebral column ripped free from the carcass and
108 curved into its new position. Chellouche et al. (2012) mooted the possibility that a similar process
109 could explain the occurrence of isolated caudal fins of fish in the Wattendorf Plattenkalk (Upper
110 Kimmeridgian, southern Germany); the fin had been "overgrown by a microbial mat or was sticking
111 to the sediment for other reasons" (op cit. p. 111). If only part of the caracass becomes adhered
112 other parts can lift off the surface and disarticulate *in situ* (see Hellawell and Orr, 2012). Peñalver et
113 al. (2002) attributed the unusual patterns of completeness and articulation exhibited by insects
114 preserved in Miocene lacustrine sediments to parts of the carcasses having become adhered to
115 microbial mats on the lake floor. Subsequently, currents removed or displaced those parts not
116 adhering to the mat, leaving the fossils incomplete but with the remaining parts preserved in life
117 position.

118 The former presence of microbial mats is relatively easy to identify in carbonate successions.
119 In vertical section there may be thin organic laminae that anastomose and interconnect over short
120 vertical distances; other biosedimentary structures include roll-up structures (see for example
121 Simonson and Carney 1999, figs 3A-B, 4, 5). Even if degradation of the organic matter is complete,
122 (typical of siliciclastic settings) the former presence of microbial mats is often revealed by various
123 sedimentary features. Bedding surfaces often exhibit distinctive textures (microbially induced
124 sedimentary structures (MISS)) (Noffke 2010; Noffke and Chafetz 2012).

125 Some of the fossil examples examined in the course of this study show no obvious indication
126 that the surface of the sediment was covered in a microbial mat. Examples of stick 'n' peel originate
127 via various other mechanisms. During decay, carcasses may become covered by a localised microbial

biofilm that may extend beyond the periphery of the carcass (see Borkow and Babcock 2003, figs 1 and 2). In other examples, non-biomineralised tissues such as the integument may be infested, even pseudomorphed, by microbes (Redelstorff and Orr 2015). Potentially, the microbes in such biofilms may play a role in stick 'n' peel, for example via the production of extracellular polymeric substances (More et al., 2014) that locally coat the organism's tissues and the substrate and bind each to the other.

The localised growth of this microbial population will be facilitated by the decay products generated by autolysis and putrefaction of the carcass (purge fluids) leaking downwards and outwards from the carcass into the substrate. This is analogous to the cadaver decomposition island (CDI) of Carter et al. (2007, p. 12), a "highly concentrated island of fertility" centred below, and extending lateral to, a decaying carcass. The CDI originates in two steps. In the first (the "bloated" phase *sensu* Carter et al. 2007) purge fluids exit via orifices (mouth, nose, anus). In the following stage, "active decay", substantial release of cadaveric fluids connects the isolated islands that formed previously, and the CDI becomes established. These fluids may also serve to bind the carcass to the substrate. There is conclusive evidence that such fluids can bind a carcass to the substrate in subaerial settings. Bickart (1984, p. 527) attributed the adhesion of bird carcasses to the substrate to "possibly a combination of body fluids and ground moisture"; floodwaters passing over these carcasses subsequently failed to change the position of most. The escape of fluids from the interior of decaying carcasses is extremely common, suggesting stick 'n' peel is potentially a recurrent taphonomic feature of vertebrate fossils.

There is also evidence that non-biomineralised tissues decaying in permanently subaqueous settings can become stuck to the surface on which they are lying, at least under experimental conditions. The examples in Figure 1 are experimentally decayed specimens of the medusa *Aurelia aurita* (Adler 2013; see also Hertweck 1966).The specimens are right-way up, with the exumbrellar surface upwards. In the specimen in Figure 1A the ventral parts of the lower surface (the oral arms) are in contact with and have become stuck to the floor of the experimental vessel. The umbrella remains free-floating in the experimental tank; it is positioned centrally above the oral arms (Figure 1A, upper image). As decay progresses minimal disturbance of the experimental vessel is sufficient to tear the umbrella (the circular outline indicated by an arrow in Figure 1B) from the remainder of the body and offset it laterally. Other experimental studies have also recorded that carcasses decaying in fluids can become adhered to surfaces inside the experimental vessel. Freidman (1999, p. 37-38, Figures 16 and 17) experimentally decayed specimens of the hagfish *Myxine glutinosa* in

containers filled with water; a number of the decayed specimens stuck to the floor of the vessels either locally or along most of their body surface.

How the distribution of the decay fluids are affected by continuous current activity and a sediment substrate (as opposed to the solid floor of an experimental vessel) are unknown, but amenable to experimental testing. Decay fluids will settle downwards inside the specimen and from there leak into the underlying substrate. The effects of current activity may therefore be limited and the decay products not dispersed into the overlying water column. The binding effects of the decay fluids would presumably be influenced by the porosity and permeability of the sediment.

3. Indicators of stick 'n' peel in fossils

We have identified a series of features indicative of stick 'n' peel, one or more of which a vertebrate fossil will exhibit if its disarticulation and loss of completeness was controlled, at least in part, by this mechanism. Schematic illustrations of these features using generalised vertebrate bodyplans are shown in Figure 2, and candidate examples of fossil taxa in Figure 3.

3.1 Displacement of an articulated part of the skeleton beyond the body outline

In many exceptional biotas the body outline of vertebrate fossils is preserved, often as a dark-coloured carbonaceous stain or a thin film that represents the degraded remains of the non-biomineralised tissues. Part of the skeleton, for example a limb or the tail, may be articulated and connected with the remainder of the skeleton but occur outside the body outline (Figure 2A, 3A). While lying on the substrate, this part of the skeleton moved into a position other than that in which it came to rest initially. Before it did so, the body became sealed to the substrate and thus remained *in situ*. In examples where the tail is moved to a new position, current activity or contraction of the tissues connecting successive vertebrae (see Seilacher *et al.* 1985) could produce the same result. As there is no disarticulation, stick 'n' peel that occurs via this process is only apparent if the body outline is preserved (as in the example in Figure 3A). If the body outline is not preserved the process can only be identified if it results in disarticulation at a joint, for example, if the distal part of an appendage such as the tail or a limb remains *in situ* and the part proximal to it moves to a new position (Figure 2B; see also Viohl 1990, fig. 2). In such cases, the original continuity of the appendage should be recovered if the displaced part is moved back to its original position.

3.2 Localised variations in disarticulation and loss of completeness within a skeleton

In this scenario, part of the skeleton shows extensive disarticulation (but not necessarily loss of completeness) and the remainder is complete and fully articulated.

In the example in Figures 2C and 3D, the anterior and posterior halves of the skeleton are juxtaposed; in the fossil frog (Figure 3D) the body outline of each half is also juxtaposed. In each example, the anterior half of the skeleton is in life position, complete, and fully articulated. The posterior part is complete, out of position, and extensively disarticulated. If decay has progressed sufficiently, the effects of gravity can force bones out of their in-vivo position when a carcass settles passively onto the substrate (Syme and Salisbury 2014). In the case of the example in Figure 2C and 3D, disarticulation did not occur when the carcass came to rest on the substrate (or both the anterior and posterior parts would have disarticulated to the same extent). Thus disarticulation occurred later, after decay had progressed sufficiently to weaken or remove the tissues (muscles, ligaments and tendons) connecting the bones. The process responsible must explain two phenomena: disarticulation of only the posterior half of the specimen, although the anterior half would have been decayed to the same extent; the movement of the posterior half as a unit, plus retention of all its skeletal elements. The second feature would be easiest while the skeleton was enclosed inside the integument (as seems likely to have occurred in the fossil example in which the body outline is preserved). The posterior half either rotated laterally, or flipped vertically, over the anterior half during current activity. Definitive evidence for it having flipped would be if the opposite surfaces of two skeletal elements were exposed on the same bedding plane; for example, the dorsal side of the skull and the ventral face of the pelvis. Only the anterior of the specimen may have been fixed to the substrate before the posterior half was moved to its new position. Alternatively, the carcass may have also have been fixed locally at other points, but ripped free. This possibility cannot be rejected on the evidence presented in the specimens in Figure 2C and 3D. It would be the preferred option if any of the skeletal elements from the posterior of the skeleton were still in their original position. This scenario is shown in the theoretical example in Figure 2D in which the articulated distal part of the left hindlimb has remained behind in life position.

Figure 3B is of the skeleton of the holotype of the bird *Primotrogon wintersteini* described by Mayr (1999, p. 430) who noted its unusual taphonomy. There are marked discrepancies in the degree of completeness and articulation between different parts of the body. Both forelimbs are fairly complete (the phalanges are absent) and articulated. They, plus the left hindlimb are in life position relative to each other. In contrast, other parts of the skeleton are either incomplete (e.g. the vertebral column) or absent (the right hindlimb and tail). Mayr (2001) described a second specimen of *Primotrogon wintersteini* noting the unusual combination of its feet being articulated and preserved in life position, but the absence of the tibiotarsi, femora and caudal part of the trunk (Figure 2C). The vertebral column is present but disarticulated. The proximal parts of the forelimbs are articulated and in life position; the distal parts are truncated by the edge of the slab.

Both specimens exhibit the combination of (1) moderate to high completeness, (2) extensive disarticulation of specific parts of the body, plus (3) limited, or no, disarticulation of those parts of the skeleton that remain in life position relative to each other. Many of the bones present but displaced from life position did not disarticulate when the carcass settled to the sediment surface; for example, the more distal parts of the forelimbs would have been unlikely to remain in life position if elements such as the coracoid and scapulae were extensively displaced at the time of deposition. Skeletal elements that are absent were not lost while the carcass floated in the water column, i.e. in the interval between death and coming to rest on the sediment surface; most obviously, it would not be possible to retain the distal part of the hindlimbs but not the proximal parts. The specimens settled onto the sediment surface shortly after death before decay had progressed significantly; most, perhaps all, of the disarticulation and loss of completeness they experienced happened subsequently. Mayr (2001) concluded that current activity might have removed the bones of the pelvic region and the proximal part of the legs of the specimen in Figure 3C; he (op cit.) envisaged that the distal part of the hindlimbs remained *in situ* as they had become adhered to the sediment. This conclusion is supported here and also suggested as the reason why the wings are articulated and complete in both specimens.

The taphonomy of each specimen would have differed in detail, but a general model can be erected. In the first step each bird came to rest with one forelimb either side of the body. This would have presented the bones of these limbs close to the sediment surface. Other parts of the skeleton would have been more elevated above the substrate, especially if the body was oriented ventral side downwards. These bones would only have moved adjacent to, and eventually onto, the substrate after a period of decay during which the skeleton collapsed. Therefore, if the carcass became stuck to the substrate and disturbed by a current before any such collapse, those parts of the skeleton closest to the substrate at the time of deposition would experience least disarticulation and loss of completeness. The high degree of articulation and completeness of the wings is thus interpreted to indicate their having being stuck to the substrate when the carcass was disturbed. The two specimens differ as to which bones of the hindlimbs are present. In the specimen in Figure 3B, the left hindlimb is complete and articulated and the right hindlimb absent; only minimal tilting of the posterior of the specimen at the time of deposition would be required to leave one limb resting on, and the other above, the substrate (see section 3.4). In the specimen in Figure 3C the distal parts of the limbs are present, articulated and but their proximal parts are absent. This may imply that the legs were flexed vertically along their length while the specimen rested on the substrate. The podotheca may have increased the likelihood of the distal parts of the hindlimbs

remaining an articulated unit (see Casal et al. 2013), but alone would not have ensured they remained in life position. The right limb is in life position.

3.3 Unpredicted loss of skeletal elements

It may not always be possible to predict *definitively* which elements of any skeleton would be affected preferentially by current activity (see section 1). Nonetheless, on the basis of their shape, density and, especially, size, it is possible to suggest which elements would be more likely to be affected than others For example, the smaller bones of a carcass (such as vertebrae and phalanges), should be transported preferentially compared to larger elements (e.g. the femora and humeri). Stick 'n' peel may, however, 'trump' this general rule, and should be suspected when elements considered more likely to have remained *in situ* and in life position are those that are displaced and removed. The example in Figure 2E is of a limb in which the distal part, including the phalanges, is articulated, complete and in life position relative to the remainder of the carcass; the humerus is missing. It is difficult to envisage a scenario where current winnowing would selectively remove the humerus, yet leave the phalanges not just present, but fully articulated. It is therefore envisaged that the distal part of the forelimb, but not the humerus, was adhered to the substrate. This theoretical example is similar to the example of *Primotrogon wintersteini* in Figure 3C, in which the distal parts of the left hindlimb, including the phalanges, are present and articulated, but more proximal bones, including the relatively large tibiotarsi and femora, are missing.

Trewin and Davidson (1996) observed rare examples of the acanthodians *Climatius* and *Ischnacanthus* in which the fin spines, notably the pectorals, are in life position, but the body scales almost totally absent. The spines are among the larger individual elements. They would be unlikely to be removed preferentially. It is also unlikely that their mass alone would result in their remaining precisely in life position while every other element was removed or displaced. It is more likely that, as Trewin and Davisdon (1996) suggest, the spines became stuck to the substrate; the build-up of gas inside the decaying carcass may have lifted the remainder above the substrate and it was removed by weak currents.

3.4 *Higher fidelity preservation of the lower facing side of a specimen*

Taxa that are strongly laterally compressed often come to rest on the sediment surface in lateral aspect (many fish, for example). This orientation presents the sagittal plane through the body parallel to the substrate. Vertebrates are bilaterally symmetrical either side of this plane. The taphonomy of paired elements that are identical in size, shape and density can be compared directly. The stick 'n' peel model predicts that the side in contact with the substrate will become

adhered to it and is the more likely to retain skeletal fidelity when the specimen is subjected to current activity.

In specimens preserved in lateral aspect stick ‘n’ peel could result in differences in the fidelity of preservation between the left and right sides of the body, for example in the completeness and articulation of the limbs and/or ribs (Figure 2F). In the example in Figure 2G (see also Figure 3E), the head of the fish is disarticulated completely, but otherwise, it is almost exclusively the relatively large, deepened, flank scales from one side of the body only that are displaced or absent. The tail of the fish in Figures 2G and 3E is entire. The tail comprises some of the smallest skeletal elements that should be among the easiest to transport; note their size relative to that of the flank scales and operculum in Figure 3E. Furthermore, the tail is at the distal end of the animal and fully exposed to any currents. The latter observation falsifies the possibility that the side in contact with the substrate is more articulate and complete simply because it was protected from the effects of current activity by the scales from the opposite side of the body without being stuck down.

4. Discussion

The theoretical models and fossil examples reviewed above suggest that stick ‘n’peel could potentially be recognised in fossils by a number of diagnostic taphonomic features. These features include loss of completeness and articulation in certain areas of the body, although other parts of the skeleton remain complete and fully articulated. This is most apparent when the left and right hand sides of a body in lateral aspect are preserved differently. Differences in completeness and articulation can occur over short distances and be subtle, for example, the displacement or absence of a single bone either side of which the adjacent bones are present and in life position. The argument that this is due to stick ‘n’ peel is strengthened if the absent skeletal element would be predicted to be present on the basis of its (larger) size, (greater) density, or shape.

The criteria for recognising stick ‘n’ peel should, however, be used with caution. Problematically, some of the patterns of disarticulation and completeness characteristic of stick ‘n’ peel can also originate via other processes. Unusual patterns of disarticulation and loss of completeness do not automatically imply that the carcass became adhered to the substrate.

For any carcass resting on a substrate, the bones on the lower facing side will be more difficult to dislodge from life position. As a carcass decays and collapses skeletal elements on the lower facing side will rotate *in situ* to more stable orientations than those at which they came to rest. These elements may separate from each other, but any displacement is likely to minimal.

Elements on the upper side of a carcass are more likely to be displaced. This displacement can occur as bones slide downwards under gravity into more stable orientations. Gravitational sliding has been documented in elephant carcasses decaying subaerially (Haynes 1988), and can result in marked differences in articulation between the left and right sides of a carcass lying in lateral aspect. On its own the process should not result in loss of completeness.

The animal's anatomy, in combination with the orientation in which the specimen comes to rest, can impact on the extent of disarticulation. Bones that are at a high angle to bedding when the carcass comes to rest may become disarticulated as the skeleton collapses downwards as it decays. For example, articulated skeletons of anurans are preserved almost exclusively in dorso-ventral aspect (although unless the way up of the specimens is known the specific orientation cannot be determined (McNamara *et al.* 2012)); often each limb is lateral to the body. In these postures most of the skeletal elements are presented parallel to bedding and close to the sediment surface in highly stable orientations. If there is no disturbance after deposition, anuran skeletons routinely show a high degree of articulation. The urostyle, ilia, and sacral vertebra, however, are often an exception. These form a three-dimensional, prism-like structure at the core of the body; these bones invariably disarticulate from each other as each rotates parallel to bedding in response to decay-induced collapse and sediment loading during burial. There are criteria by which disarticulation due to decay-induced collapse can be distinguished from stick 'n' peel. Decay-induced collapse results in limited displacement (as each element is likely to remain inside the body outline) and does not result in any loss of completeness. Stick 'n' peel is most obvious if it involves loss of completeness and displacement of elements is over larger distances. Decay-induced collapse will affect specific joints and the effects will be the same for all specimens in the same posture. The same need not be the case for disarticulation resulting from stick 'n' peel; this depends on the timing of current activity relative to how far decay has progressed. The taphonomic features produced via stick 'n' peel need not therefore be consistent between specimens within an assemblage, even those of the same taxon.

One of the distinctive features of stick 'n' peel is that there are highly localised differences in completeness and articulation within a specimen. A limited number of other processes can produce spatial variation in the fidelity of preservation within a single specimen, for example abdominal rupture, as a result of the explosive release of decay gases. This will reduce the skeletal fidelity of the thorax and abdomen; other parts of the skeleton are less likely to be affected.

Not all skeletal elements in a vertebrate carcass have equal fossilisation potential. Less well-ossified elements are likely to dissolve preferentially during early diagenesis. Complete decay or

dissolution of a skeletal element before sediment lithification would result in no mould to indicate its former presence. Skeletal completeness can therefore be strongly sensitive to developmental stage and the pattern of ossification during ontogeny. Alternatively, decay microenvironments that are conducive to the dissolution of bone may develop locally within a carcass, for example, inside the body cavity (see McNamara et al. 2009). As a result, the fossilization potential of skeletal elements may differ between parts of the body. The specimen of the bat *Palaeochiropteryx tupaiodon* illustrated by Franzen (1990, fig. 2) lacks any bones in the body cavity, but is otherwise complete and highly articulated (limited disarticulation of the tail has occurred). The absence of bones inside the body was attributed to their having dissolved during diagenesis.

5. Stick 'n' peel: limitations of a predictive model

Whether stick 'n' peel occurs depends on when skeletal elements become stuck to the substrate relative to the timing of the current activity responsible for their displacement and removal. When skeletal elements become stuck to the substrate depends on the interaction of two variables: rate of collapse of the carcass; rate at which the CDI builds up, then dissipates (Figure 4). Firstly, as decay progresses, the muscles, ligaments and tendons that hold the skeleton together lose mass and strength; the skeleton will progressively collapse downwards under its own weight. Individual bones will rotate into more stable positions than those in which they were originally deposited, presenting more of their length or surface area parallel to the substrate. Over time, therefore, progressively more bones move closer to, and, ultimately, rest on, the substrate. Secondly, the areal extent and volume of the CDI will initially increase, but then decrease as the decay purge is metabolised and disperses. Three fields can be defined over time (Figure 4). In stage 1, during the initial stages of decay, the volume of the CDI is limited and collapse of the skeleton minimal. Current activity will either transport the entire carcass or have limited impact on the skeletal fidelity of a carcass that remains *in situ*. In stage 3 the extent of the CDI will be limited and the carcass will have been reduced to individual, or co-joined, bones. Which skeletal elements are displaced and removed will be governed largely, possibly exclusively, by their hydrodynamic properties. The effects of stick 'n' peel on skeletal fidelity will be most pronounced during Stage 2. During Stage 2 the volume of the CDI will change and collapse of the skeleton will be on-going. Differences in completeness and articulation will result depending on the timing of current activity.

It is difficult to model what may happen in any more detail, as a number of other variables are involved. How the skeleton collapses will reflect the animal's anatomy and the orientation of the carcass. The rate at which decay progresses and, linked to it, the rate at which purge fluids are generated and metabolised, will be controlled by environmental conditions (including temperature

and oxygen levels). The geometry of the CDI and how long it will persist are both difficult to predict. There is no reason to assume the CDI will retreat from its periphery inwards, and persist longest centrally. It is likely that it would be most dense and persist longer in proximity to the orifices such as the mouth and anus and other sites (wounds) via which the decay purge exited the body. The geometry of the CDI will also be sensitive to the orientation the carcass came to rest in. The nature of the substrate is potentially important. Carcasses would presumably be more likely to adhere if the substrate has some, but limited, permeability, as this will inhibit the diffusion of the purge fluids downwards.

6. Wider Implications

The various fossil examples presented indicate the phenomenon of stick 'n' peel is likely to be a common feature of the taphonomic history of vertebrate fossils deposited on either a subaerial or subaqueous substrate. There are implications for various other aspects of vertebrate taphonomy. Inferences as to the extent of bottom water current activity based on the degree of completeness and articulation of fossils should be made with caution. Limited disarticulation and near full completeness need not imply that bottom water currents were absent. Instead, specimens that adhered to the substrate may have been resistant to the winnowing effects of currents.

Carcasses that become buoyed up by decay gases may refloat after initially sinking. The reasons whether they refloat or do not are complex; the biology of the organism, and the temperature, density and depth of the water (and thus the hydrostatic pressure) are important variables (see review by Reisdorf et al. 2012). The preservation of complete, fully articulated, skeletons is often attributed to environmental conditions that inhibited scavenging, and the water pressure having been high enough to have prevented refloating. Refloating could also be inhibited if a carcass became stuck to the sediment-water interface. Problematically, in the absence of any disarticulation and loss of completeness (i.e. if the 'stick' component occurs but not the 'peel') there may be no evidence in the fossil that the carcass had adhered to the substrate.

It is likely that stick 'n' peel is also an important part of the taphonomy of invertebrate fossils. The effects of stick 'n' peel will be most apparent in invertebrates with multi-element skeletons, for example echinoderms. Possible examples occur in assemblages of the crinoid *Uintacrinus* described by Meyer and Milsom (2001). The assemblages represent *in situ* mass mortalities of opportunistic taxa that colonised persistently low-oxygen to anoxic environments during brief episodes of oxygenation. Mortality occurred as a result of anoxia not obrution. Carcasses were therefore exposed on the seafloor after death and buried subsequently. Meyer and

Milsom (2001) observed that the downward-facing side of an individual calyx can be highly-articulated and complete, yet the opposite side extensively disarticulated. At a larger scale, an *Uintacrinus* layer routinely comprises disarticulated crinoidal material on its upper surface, but crinoids with articulated calyxes and arms on its lower side. Meyer and Milsom (2001) attributed this unusual combination of preservational states to a microbial mat of necrolytic origin having grown over the crinoids early in the decay process. The cohesive properties of this mat held disarticulated ossicles in place on the upper surface of a layer and prevented their being dispersed by bottom currents. The occurrence of the latter is indicated by the parallel alignment of *Uintacrinus* arms and baculites on some slabs. There is now no evidence for such a microbial mat on the upper surface of the crinoid layer; Meyer and Milson (2001) suggested it degraded before being covered by sediment. Remnants of organic matter persist within the crinoid layer as thin organic laminae. Meyer and Milson (2001) suggested these represented microbial mats, or organic matter exuded from the compressed calyxes. If the latter, the decay products would presumably have leaked downward under gravity, and may have 'glued' skeletal elements in position inside the layer. This would have enhanced the likelihood of these parts of skeletons remaining articulated and, contributed to the discrepancy in the fidelity of preservation between the opposite faces of both single specimens and a layer of crinoids as a whole.

The body outline of the specimen of *Apateon pedestris* in Figure 3A remained entire and *in situ* when the vertebral column rotated into its new position. More generally, it is not uncommon for integumentary structures such as hair and feathers to be retained in life position in exceptionally preserved fossils; the inset in Figure 3B shows the outline of the feathers of the holotype of *Primotrogon wintersteini*. Fossils can exhibit these features even though their skeletons disarticulated and lost completeness while resting on the sediment-water interface. It is conceivable that the integumentary structures are retained in life position because they became adhered to the sediment surface they were lying on. The possible role of this in the taphonomic history of exceptionally preserved fossils merits further investigation.

7. Conclusions

Stick 'n' peel refers to the distinctive patterns of disarticulation and loss of completeness that result if vertebrate carcasses become adhered to the substrate in the initial stages of decay and are then disturbed by water currents. It has long been known that carcasses can adhere to microbial mats on the surface of the sediment (Mayr 1967, Viohl 1990, Seilacher et al. 1985). However, many fossil examples occur in sedimentary contexts that show no evidence for such mats having been present. The degraded tissues of the carcass, the associated microbiota, and especially, the decay

purge released from inside the decaying carcass, are alternative mechanisms by which carcasses can become locally adhered to the substrate. Field and laboratory experiments confirm that this occurs in both subaerial and subaqueous settings.

Retrospective identification in fossils that stick 'n' peel occurred is not straightforward. Two unusual features of the skeletal taphonomy of vertebrates may be indicative:

(1) in disarticulated and incomplete skeletons the presence of bones that, on the basis of size, shape and/or density, would be expected to have been displaced and removed, and the absence of bones that would have been predicted to be present;

(2) those parts of the carcass that can be shown on independent criteria (by knowing the way up of the specimen) to have been in contact with the substrate will be more fully articulated and complete than those that were not in contact with the substrate.

Stick 'n' peel can result in various different patterns in fossil skeletons. Problematically some of these can also originate via other mechanisms. There is sufficient evidence to confirm that the phenomenon recurs in fossil assemblages preserved in both marine and freshwater systems. Field observations confirm that it can also develop on land (Bickart 1984). Stick 'n'peel is likely to be a common feature in vertebrate fossil assemblages in which caracsses experienced an extended residence time at the sediment-water or sediment-air interface as part of their taphonomic history. The phenomenon is also likely to have affected invertebrate taxa with similar taphonomic histories preserved in the same environments. Finally, stick 'n' peel offers a potential mechanism by which the body outline, and integumentary structures such as feathers and hair, can be retained in life position in exceptionally preserved vertebrate fossils in which the skeleton is disarticulated and incomplete.

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599 FIGURE CAPTIONS

600 Figure 1. Stick ‘n’ peel exhibited by experimentally decayed examples of the moon jellyfish *Aurelia*
601 *aurita.* (A) Those parts of decaying specimens that come into contact with the bottom of the
602 experimental vessel can become stuck to it. (B) Even minimal disturbance of the experimental vessel
603 is sufficient to tear the floating umbrella from those body parts stuck to the floor of the
604 experimental vessel. When the umbrella settles to the floor of the vessel it can be laterally offset
605 from the adhered parts. Upper and lower images show corresponding planar and lateral views of the
606 same experimental vessel. The arrow in the upper image in part B indicates the margin of the
607 umbrella (Adler 2013).

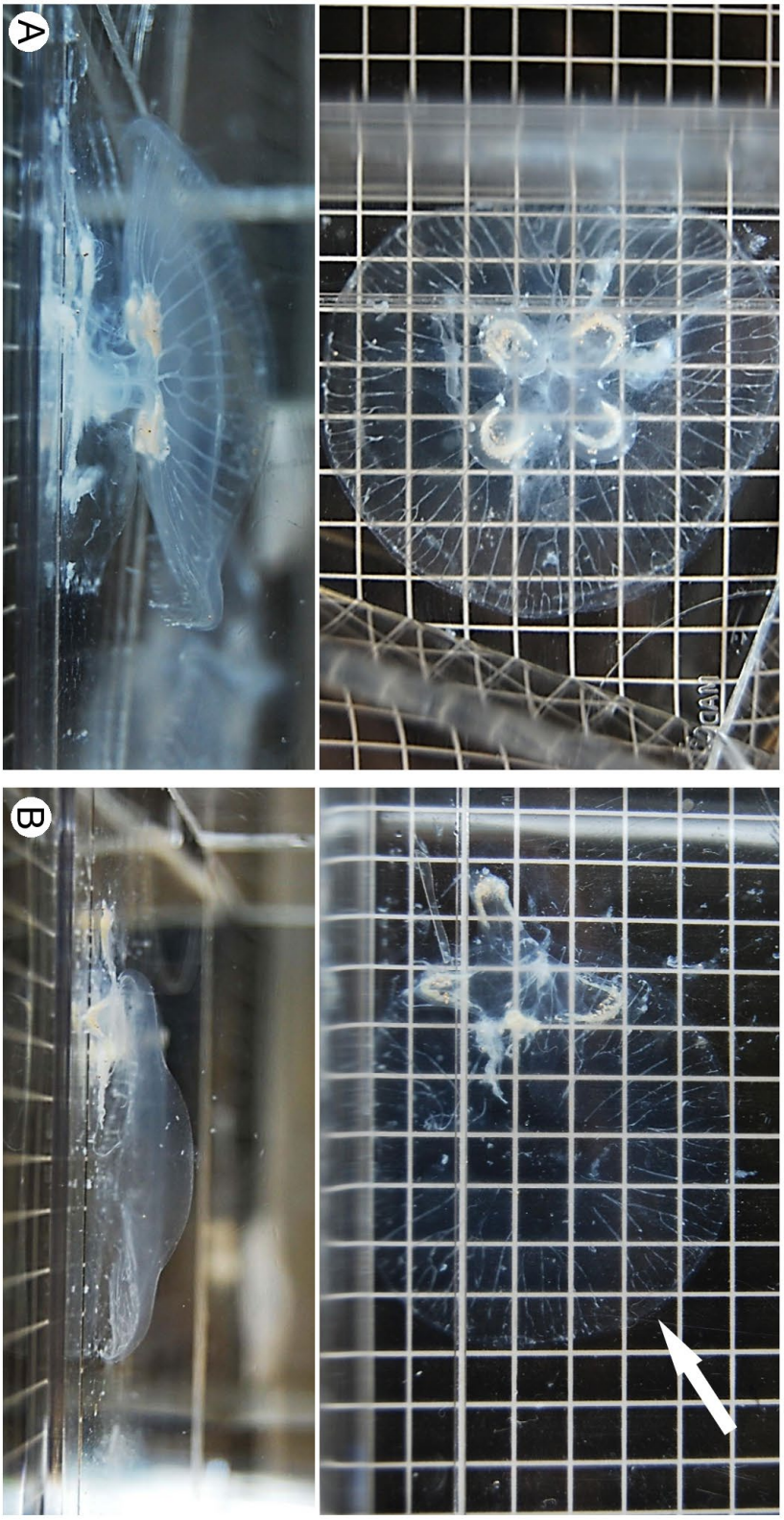
608 Figure 2. Schematic illustrations of taphonomic features that form via stick ‘n’ peel. (A) The
609 vertebral column of the tetrapod is intact but curves outside the body outline. The integument has
610 adhered to the substrate and remained *in situ* when the vertebral column of the tail rotated into its
611 new position. This evidence for stick ‘n’ peel requires the body outline to be preserved. (B) The
612 skeleton is entire and fully articulated except for one point of separation within the tail (at arrow).
613 The carcass came to rest on the substrate and the distal part of the tail (and possibly other parts of
614 the skeleton) became adhered to it. The distal part of the tail remained *in situ* when part of the
615 vertebral column rotated into a new position. The alignment of successive vertebrae was retained in
616 both parts of the tail. Note that in contrast to the example in Figure 2A, evidence for stick ‘n’ peel
617 does not require that the body outline is preserved. (C) The anterior half of the skeleton is complete
618 and fully articulated. The posterior half is complete, but extensively disarticulated and out of life
619 position. The carcass came to rest on the substrate fully articulated and complete; subsequently,
620 after an extended period of decay, the posterior part either flipped over, or rotated anticlockwise
621 onto, the anterior part. In doing so, it disarticulated. Completeness and articulation of the anterior
622 half was unaffected. On the evidence available it cannot be proven whether the anterior was the
623 only part that adhered to the substrate, or whether the specimen was also adhered elsewhere and
624 the posterior half preferentially tore free (contrast with the scenario in Figure 2D). (D) The only
625 difference in the distribution of this skeleton and that in Figure 2C is that the distal part of the left
626 hindlimb is in life position. This implies that the carcass first adhered to the surface at both the
627 anterior and at the distal part of the left hindlimb; when the posterior part tore free the latter
628 remained *in situ*. (E) The skeleton is fully articulated and, except for loss of a single humerus (at
629 arrow), complete. All elements are in life position. The isolated limb is separated from the remainder
630 of the carcass by exactly the length of the humerus; i.e. the limb did not separate from the

remainder of the carcass as a unit. The distal part of the limb (and presumably other parts of the skeleton) adhered to the substrate and remained *in situ* while the humerus was selectively removed. (F) and (G) The carcass came to rest in right lateral aspect. Only the left side of the skeleton is extensively disarticulated. Elements displaced significantly from life position include some of the largest bones, for example the left femur and humerus in F and the chevron-shaped flank scales in G. The skeletal elements that remained *in situ* share two features. Firstly, they would have been in contact with the substrate after the carcasses came to rest. Secondly, not all would have been shielded from the effects of currents by being concealed on the lower-facing side of the carcass. Those that would have been exposed include some of the smallest bones, for example the phalanges of the limbs from the right hand side of the body and the distal vertebrae of the tail in F, and the bones of the caudal fin ray in G.

Figure 3. Examples of fossil taxa interpreted to show taphonomic features derived via stick 'n' peel. (A) Specimen of the amphibian *Apateon pedestris* (Museum für Naturkunde Berlin: Institut für Palaontologie, MB Am1300). (B) and (C) Specimens of the early Oligocene bird *Primotrogon wintersteini.* Inset in B shows distribution of feathers. Line drawings based on Figures 1 and 2 in Mayr (2001). (B, Bayerische Staatssammlung für Paläontologie und Historiche Geologie, BSP1997I38. C, Forschungsinstitut Senckenberg Frankfurt am Main, Germany SMFAv423). c, coracoid; f, furcular; h, humerus; r, radius; s, scapula; tm, tarsometatarsus; tt, tibiotarsus; u, ulna; ub, unidentified bone; v, vertebrae; prefix l and r indicate left and right hand side of the body, respectively. (D) *Palaeobatrachus sp.* from the Late Eocene - Oligocene Ústí Formation (36.1-25.5 Ma) of North Bohemia (Czech Republic) (Natural History Museum Prague Specimen Pb684). (E) Specimen of the fish *Habroichthys minimus* from the Prosanto Formation, Early Ladinian, southeastern Switzerland (Paläontologisches Institut und Museum der Universität, Zürich, PIMUZ A/I 3733). fs, flank scales, o, operculum; pf pectoral fin; so, suboperculum. All scale bars 10mm.

Figure 4. Model for the formation of stick 'n' peel textures, indicating the potentially complex interplay of the three principal factors: (1) progressive, decay-induced, collapse of the skeleton; (2) development and then loss of the cadaver decay island; (3) the timing of any disturbance of the carcass by current activity. Factors 1 and 2 allow three fields to be defined in each of which the impact of current activity on the taphonomy of the skeleton will be different. A-E represent schematic illustrations of a generalised tetrapod showing the changes in posture, extent of collapse of the skeleton (see transverse sections through body) and the areal extent of the CDI at different times.

664 FIGURES



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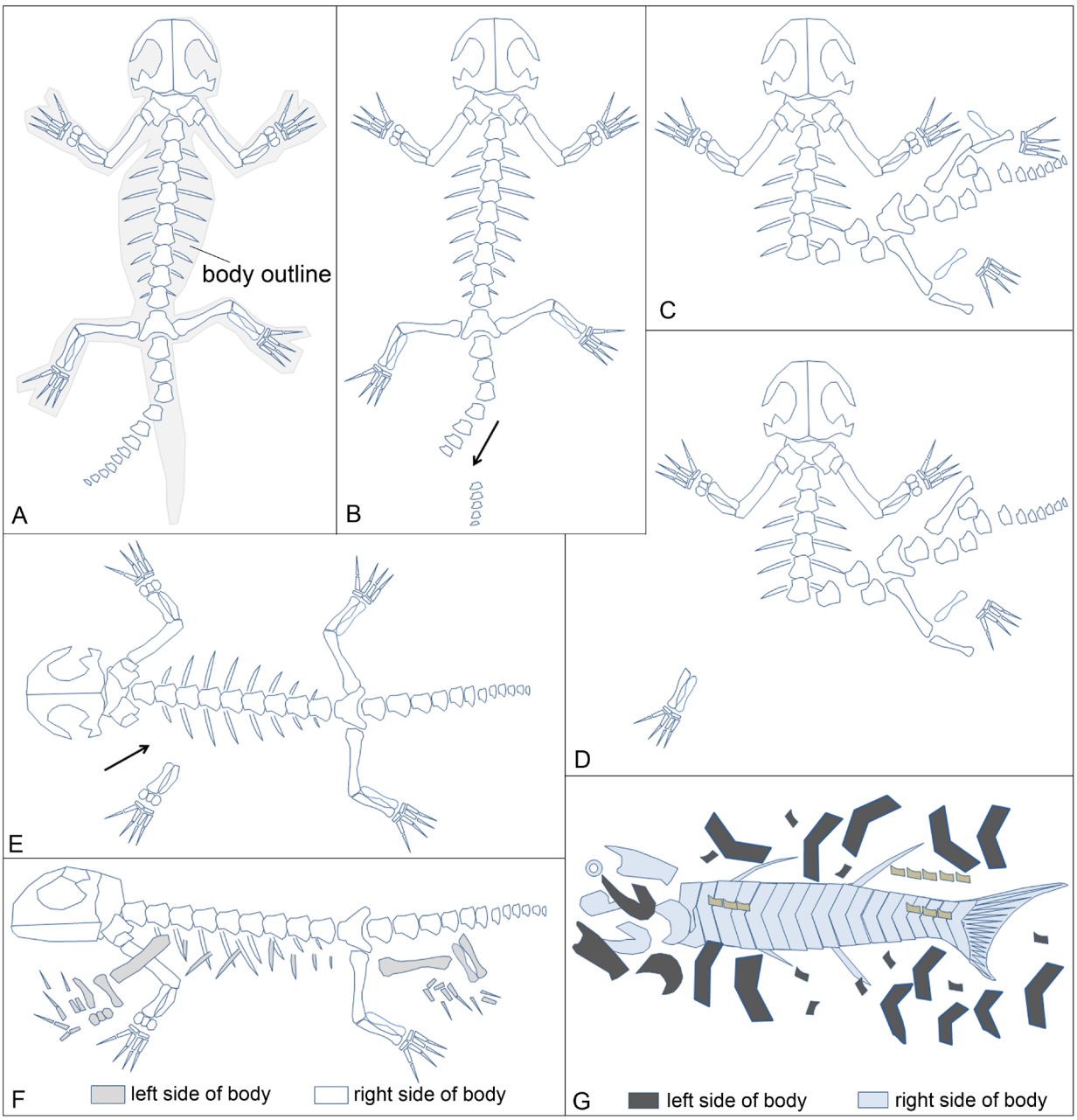
666 Figure 1



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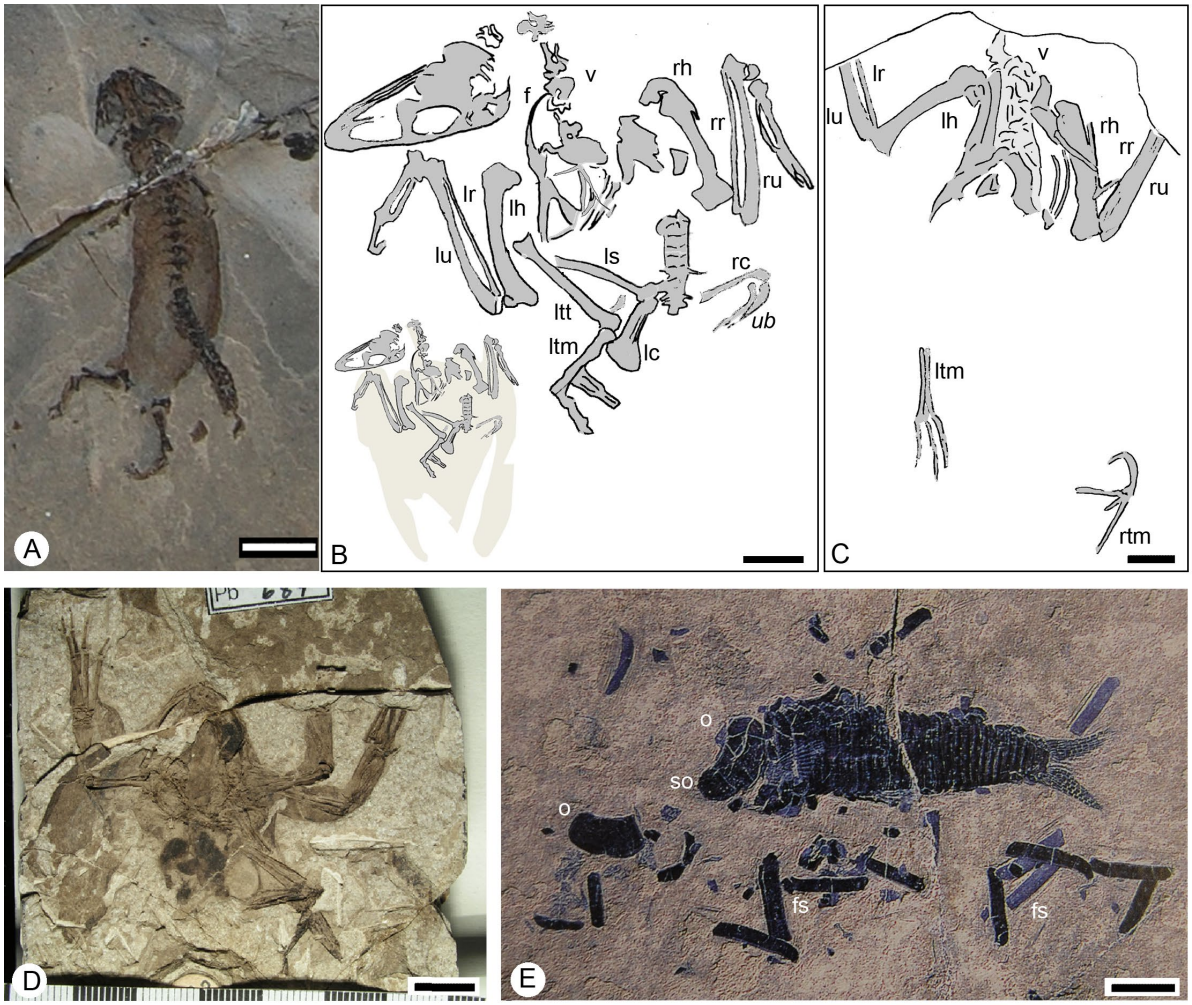

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676 Figure 3

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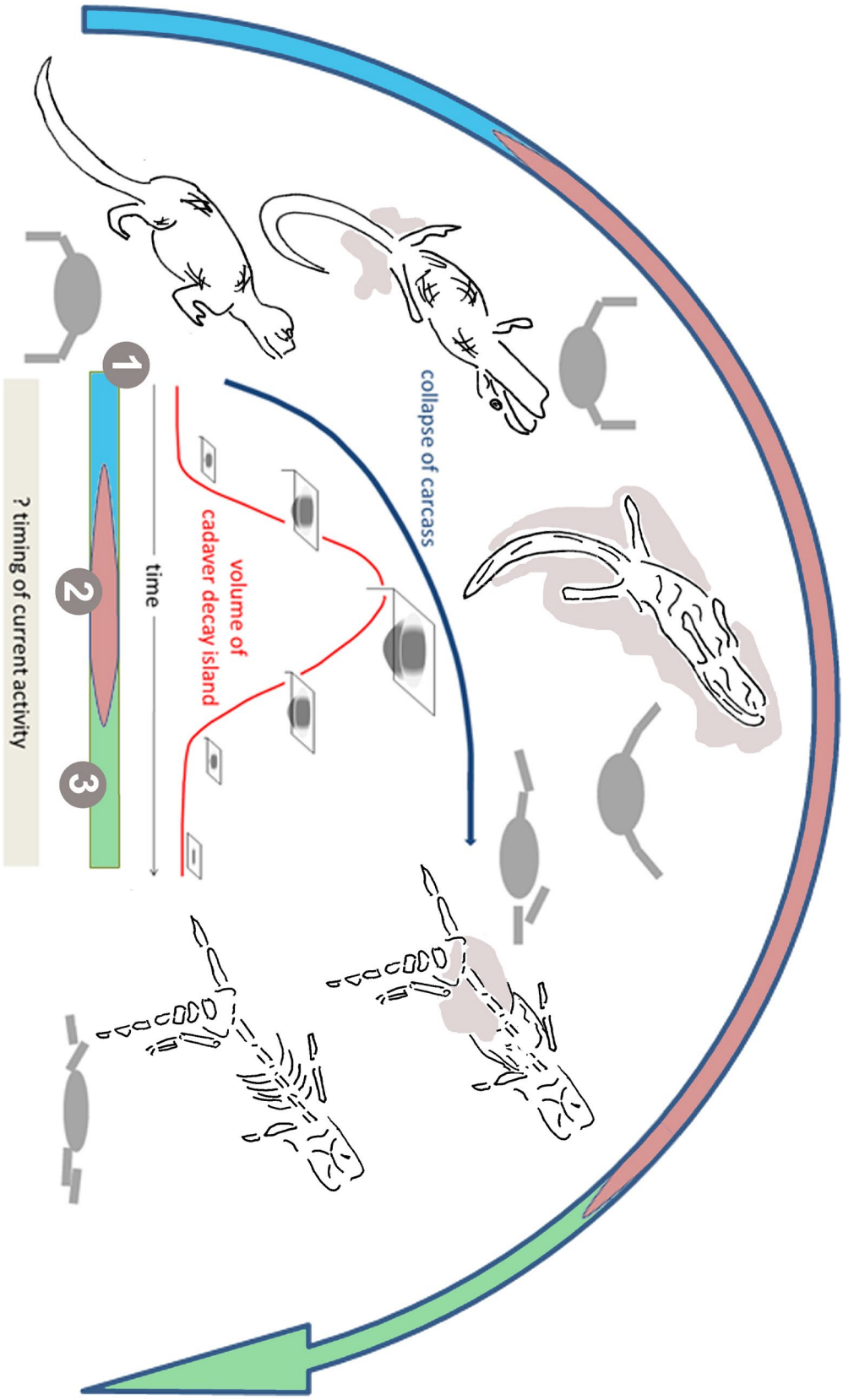

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687 Figure 4